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RESISTANCE OF PINE HYBRIDS TO THE PINE REPRODUCTION WEEVIL

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U. S. Department of Agriculture

A cooperative study by the Forest Insect Laboratory
and the Institute of Forest Genetics,
California Forest and Range Experiment Station

* MAINTAINED AT BERKELEY, CALIFORNIA, IN COOPERATION WITH THE UNIVERSITY OF CALIFORNIA.

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INTRODUCTION

The United States is entering the era when second-growth and planted trees must meet the Nation's timber requirements. Indeed much of the timber harvest east of the Rocky Mountains already is from second growth. This has required many adjustments in logging, milling, and marketing methods. It also required an adjustment in forest insect control. Heretofore, the forest entomologist has been concerned mainly with protecting mature and overmature stands until they could be harvested. There is still much to be done in this field, but the insect problems of juvenile tree stands will become increasingly important as time goes on.

There are two basic ways of approaching these problems. In one, the entomologist might study different methods of controlling insect epidemics in young stands. The second approach would be to combine forces with the forest geneticist in an attempt to breed forest trees resistant to insect attack.

A start toward determining the capacity of pine hybrids to resist well-known insect enemies of pines has been made at the Institute of Forest Genetics near Placerville, California, where a project is being carried on cooperatively by the California Forest and Range Experiment Station and the Bureau of Entomology and Plant Quarantine, of Berkeley, California. The study thus far has been concerned with resistance to the pine reproduction weevil (Cylindrocopturus eatoni). This insect attacks pines during the first decade or so of the young tree's growth and the weevil has been found to be first in a sequence of insect pests that attack pines during the long period of growth from seedling to maturity. The first tests on new hybrids were begun in May, 1946, and were continued during the seasons of 1946,1947, and 1948. The preliminary results of this experimental work and of studies connected with the project will be reviewed in this paper.

HISTORY OF PINE REPRODUCTION WEEVIL PROBLEM

The pine reproduction weevil first came to be recognized as an insect of considerable economic importance in connection with forest plantings in the brushfield areas of northern California. During the period from 1934 to 1940, thousands of acres were planted to ponderosa and Jeffrey pines. Before the trees were planted, the brush was cleared by bulldozing windrows through the fields so as to expose the mineral soil. This preparation of the ground increased the costs of planting. Initial survival was good. The young trees appeared to be doing well for the first two or three years, but high mortality developed in some areas after four or five years of growth. It was then found that the trees were being killed by the pine reproduction weevil. The heaviest damage occurred in the Big Springs brushfield where over 90 percent of the young trees were killed within 10 years after planting. Other areas, the Burney and Shasta brushfields, were also invaded by the weevil but here the damage was less severe.

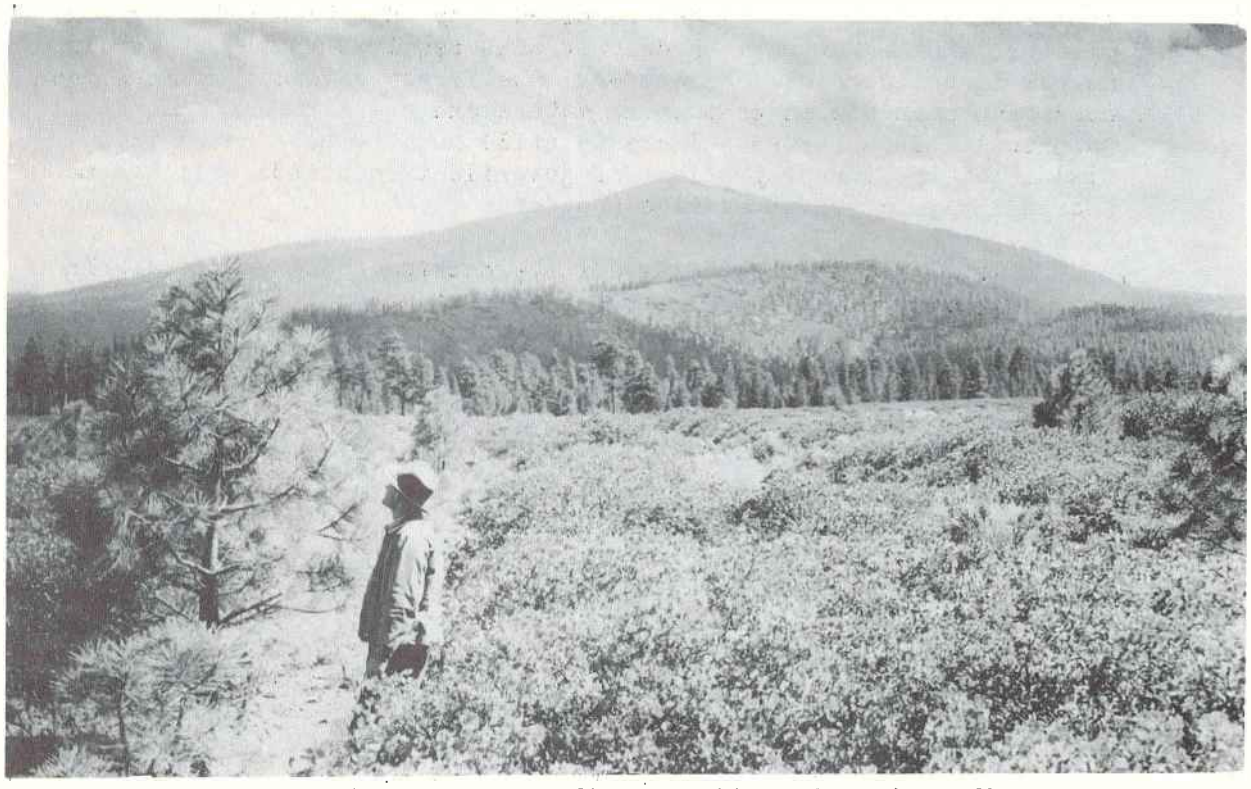

Figure 1.--Fifteen years after planting, less than five percent of the pines are alive in the Big Springs brushfield, Lassen National Forest.

This threat to investments already made in brushfield plantings stimulated an investigation by the Bureau of Entomology and Plant Quarantine. Intensive studies during 1939 and 1940 by Eaton[1/] on the biology and ecological relationships of the weevil yielded a much better understanding of the problem and provided the basis for control by the use of protective sprays. This method was not put to more than laboratory tests until 1947, when an upsurge of weevil infestations in the Shasta and Burney brushfields threatened to completely wipe out these plantations. In June of that year 500 acres were sprayed by airplane with DDT oil emulsion, and 135 acres with ground spray equipment. Control was effective in that surviving trees were protected from attack during the remainder of the season. The operation also reduced the weevil populations in the areas to such an extent that they did not again become aggressive during the two succeeding seasons.

Although direct control has thus been demonstrated to be successful, it offers only a limited solution to the weevil problem in pine plantations. Natural pine types always have an endemic population of the weevil in the reproduction of uneven-aged stands. This population is capable of building up aggressive outbreaks wherever it finds extensive even-aged stands of young trees such as occur in plantings. Hence protection of young trees cannot be assured unless spray applications are repeated each season during the period of weevil attack. Obviously, if resistant planting stock can be secured, it should cost no more to plant than susceptible stock, and subsequent high costs of protection against the weevil can be avoided.

POSSIBILITIES FOR WEEVIL RESISTANT PLANTING STOCK

Ponderosa and Jeffrey pines were selected as suitable species for brushfield plantings because of their desirable silvicultural qualities and their adaptation to the climatic and soil conditions of this region. Susceptibility of the young trees to weevil attack and the prospect for high mortality from this cause was not realized until after the plantations had been set out.

Weevil infestations that developed in the plantations demonstrated that the degree of susceptibility varies widely between individual trees in both ponderosa and Jeffrey pines. Some trees survived even when heavily attacked by the weevil in areas where the greatest damage occurred (see fig. 1). This suggests that resistant strains of ponderosa and Jeffrey pines may be developed through natural or artificial selection, but the process would necessarily be slow. A more rapid

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1/ Eaton, C. B. Biology of the weevil Cylindrocopturus eatoni Buchanan, injurious to ponderosa and Jeffrey pine reproduction. Journal of Economic Entomology 35(1): 20-25. February 1942.

approach to production of resistant strains would be through crossing a resistant pine species with a species of desired silvicultural qualities. A hybrid which would apparently meet these specifications had already been produced at the Institute of Forest Genetics at the time when these studies were started.

In 1937 a tree discovered in the San Jacinto Mountains of California was recognized as a natural hybrid of Jeffrey and Coulter pines, a cross that has since been produced by artificial pollination. In 1939 pollen from the natural hybrid was placed on Jeffrey pine conelets, and a backcross was produced. Jeffrey pine was known to be a preferred host of the weevil, but there were no records of Coulter pine having been killed by this insect. It was therefore suspected that this hybrid might possess the desired combination of inherited properties; i.e. the silvicultural characteristics and wood qualities of its Jeffrey parent along with the weevil resistance found in Coulter pine. This was the first of the hybrids to be tested against the weevil in the program of experiments and studies followed up to the close of the 1948 season. A number of other hybrids and species of pine were also tested for weevil resistance. Altogether some 21 recognized species, strains and hybrids of pines growing in the nursery and outplantings at the Institute of Forest Genetics have been studied. The results indicate that resistance to weevil attack is an inherited characteristic which can be developed by plant breeding. As will be shown later, resistance of the Jeffrey-Coulter cross was greatly improved over that of its Jeffrey parent by introduction of the resistant Coulter pine strain.

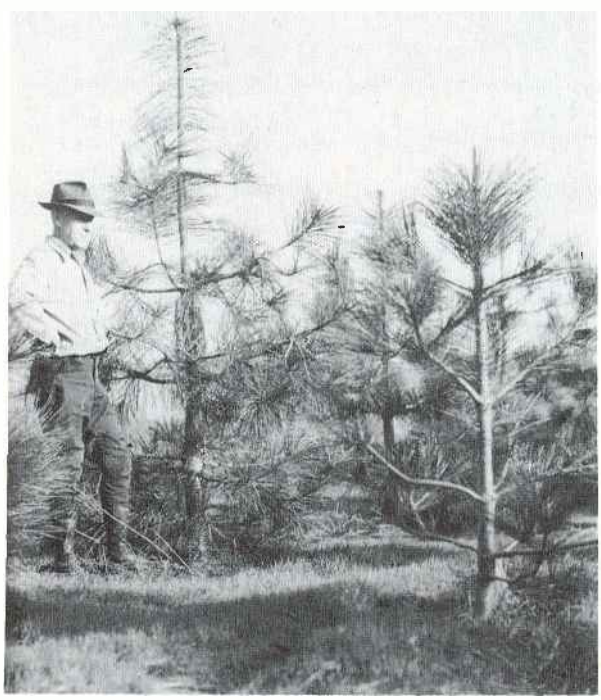


Figure 2.--At left - the hybrid, P. Jeffreyi x (P. Jeffreyi x P. Coulteri). At right - P. Jeffreyi (progeny of the Jeffrey parent). Both trees are in their sixth growing year.

HOW THE PINE REPRODUCTION WEEVIL KILLS TREES

An understanding of the nature of weevil attack is necessary to interpretation of the results of these studies. The adult weevil is a small compact insect about 2.6 mm. in length. Its body is covered with an irregular arrangement of black and white scales which give it an overall gray appearance. A prominent feature is its long, black, curved beak, typical of the weevil family. This species is capable of rapid body movements, but apparently does not fly very far. When attacking trees the adults move about mostly by crawling or hopping.

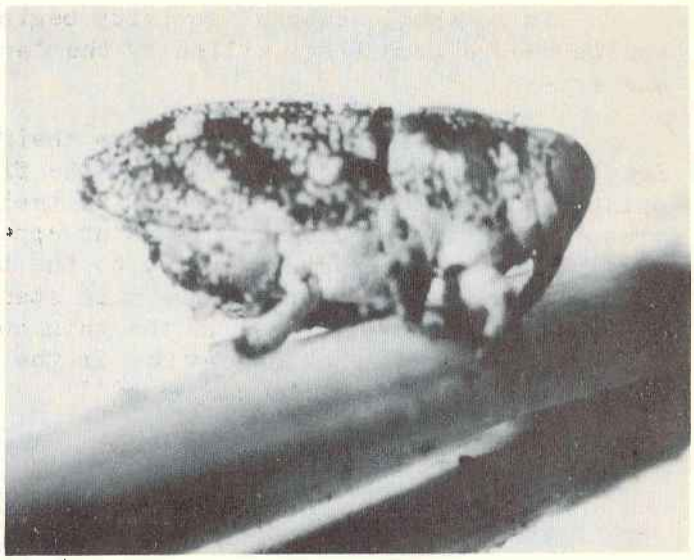


Figure 3--Cylindrocopturus eatoni, Buchanan (x 20) adult in feeding position on pine needle.

In uneven-aged pine stands the damage caused by this insect is seldom conspicuous, as only occasional small trees are killed. The weevil apparently does not thrive where the young trees are shaded by older trees in the stand. Epidemic populations of the weevil have been found only where reproduction occurs in dense even-aged stands on well exposed sites.

Pine reproduction on burned-over areas affords favorable host material for the weevil. One epidemic of this type was recorded on the Harris Ranch burn during the period 1939-1945. This epidemic died down when the surviving trees outgrew the susceptible age.

Pine plantations present similar even-aged exposed stands of young trees and thus afford favorable conditions for weevil populations.

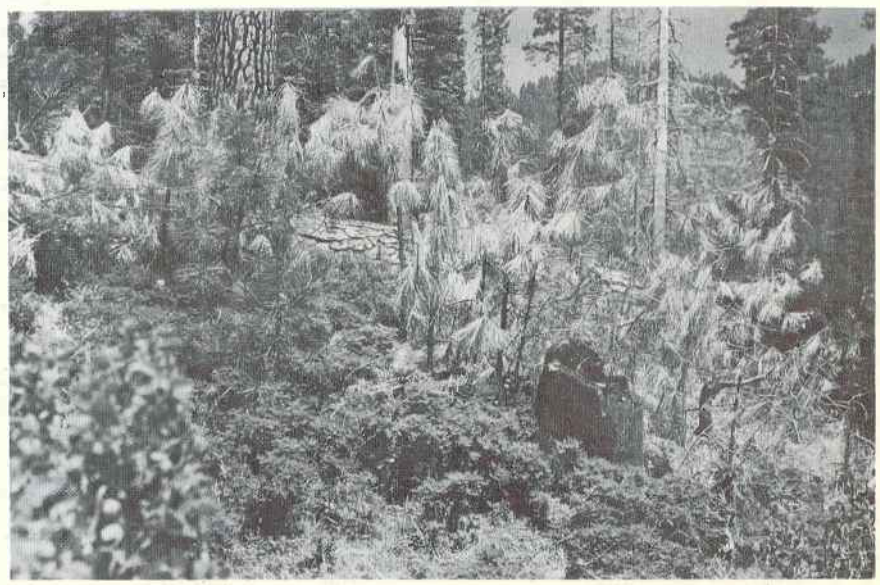
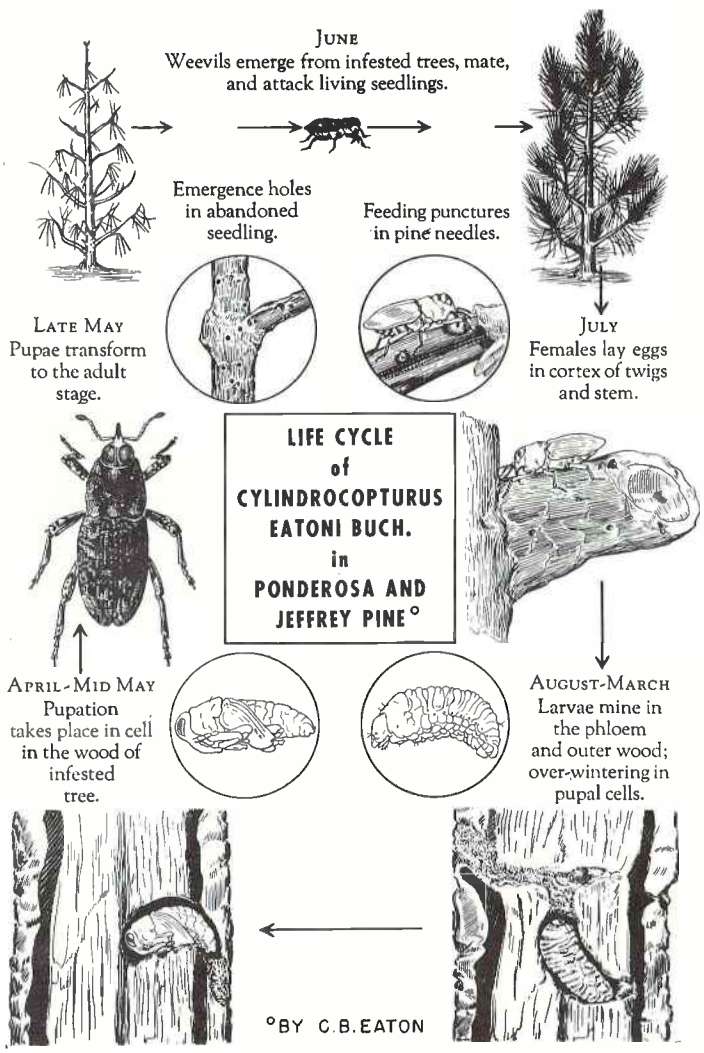


Figure 4.--Natural reproduction of ponderosa pine killed by the weevil. These young trees were restocking the Harris Ranch burn, Sierra National Forest.

The Life Cycle of the Weevil

In general, seasonal activity begins in May and June when new adults emerge from trees killed by the larvae during the preceding summer.

After these new adults emerge their first interest is in the needles of young pines. They spend the first week or so of adult existence making small punctures with their bills in the epidermal tissue of living needles. This is an apparent feeding habit which does not result in serious injury to the tree. After feeding on the needles the adults go to the main stems of the same trees. Here they make similar punctures in the thin outer bark. Under each puncture is a small hollow cavity in the outer cortex, which the weevil excavates with its curved bi''


JUNE
Weevils emerge from infested trees, mate, and attack living seedlings.
Emergence holes in abandoned seedling.
Feeding punctures in pine needles.
LATE MAY
Pupae transform to the adult stage.
JULY
Females lay eggs in cortex of twigs and stem.
LIFE CYCLE of CYLINDROCOPTURUS EATONI BUCH. in PONDEROSA AND JEFFREY PINE°
APRIL-MID MAY
Pupation takes place in cell in the wood of infested tree.
AUGUST-MARCH
Larvae mine in the phloem and outer wood; over-wintering in pupal cells.
°BY C.B.EATON

One of the first effects of the punctures is rupture of resin vessels in the outer cortex. This causes the resins to flow out to the bark surface and form small glistening beads of pitch. The amount of pitch thus produced varies greatly between individual trees and species. Trees that produce strong pitch flow appear to be somewhat more resistant to weevil attack than trees that do not, but the relationship of resin production to weevil resistance is yet to be established. It is probable that the chemical makeup of the resins is more important in weevil resistance than the volume of resin.

The stem pictured in figure 5 is on a suppressed ponderosa pine which resisted heavy weevil attack. Punctures in needles and stems and beads of pitch on the bark are the only external evidences of weevil attack on living trees. From here on the developments following attack take place entirely underneath the bark, in the layers of tissue between the outer bark and wood, and are not easily seen.

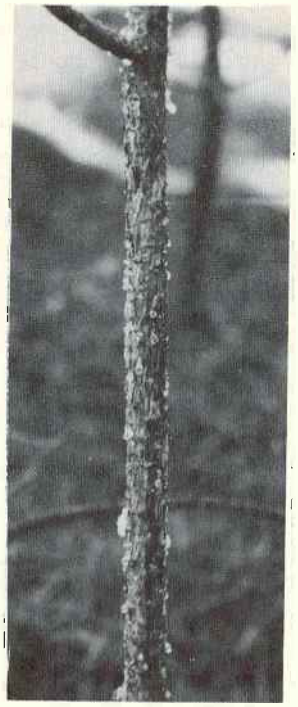


Figure 5.--Resin flow from weevil punctures on stem.

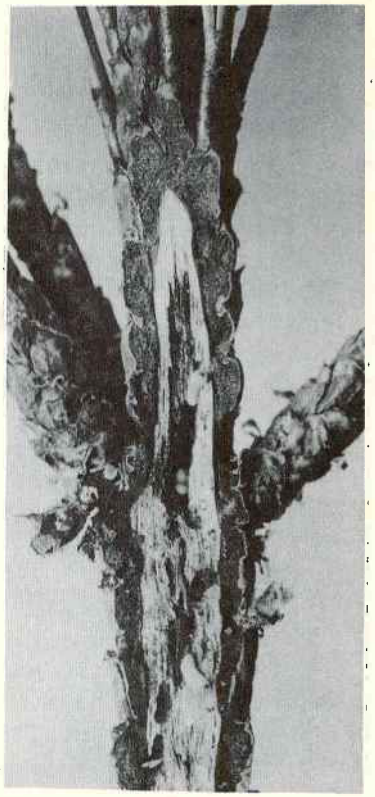


Figure 6.--Weevil larvae in dead pine stem.

Eggs are deposited in, or alongside of, punctures on the outer bark of the stem. The eggs incubate within a week or so and, if the tree is susceptible, tiny larvae extend mines into the living cortex and phloem. These larvae develop rapidly during July and August and are usually full grown by the middle of September. By this time, or soon after, the infested trees start to fade in color, the stems dry out, and the trees are dead by fall. The mature larvae bore into the sapwood where they spend the winter. In small stems the overwintering larvae enter the pitch as shown in figure 6. No further development takes place until the following spring, when the larvae transform to pupae and new adults, thus making one annual generation.

Along with this development of the weevil, certain plant processes go on within the tree itself which are highly important to the success or failure of the insect's attack. These processes will be discussed after a review of the experimental work.

METHODS USED IN RESISTANCE STUDIES

The first tests for weevil resistance were started at the Institute of Forest Genetics in May 1946. The nursery and outplantings of the Institute then contained a wide assortment of pine species, strains, and hybrids of suitable age for weevil attack. Many nursery beds were fully stocked with trees of ages up to seven years. These nursery beds made excellent settings for test cages, especially those in which hybrids were planted in rows adjacent to seedlings from their cone-bearing parents, thus making it possible to test both strains under identical conditions.

The first tests for resistance to weevil attack were made by exposing the trees to weevil populations of sufficient number to make strong attacks on the bark surface of the living stems. In order to speed up the experiments the expedient of enclosing selected trees in cages with large numbers of adult weevils was adopted because there was no assurance that uncontrolled weevil populations in the field would be strong enough for adequate tests. To wait for such uncaged populations to increase would leave much of the program to chance and involve long delays. Another consideration was the necessity for keeping weevil infestations in the vicinity of the Institute under control in order to avoid the risk of losing many valuable trees not included in the resistance tests.

Under cage controls only a limited number of trees could be used in any one test. Trees were selected in small groups in the nursery beds and weevil-tight cages were fitted around them. Several types of cages were developed but the one illustrated here was the most satisfactory.

Surgical gauze (28 mesh) was fitted over a wooden framework. On the north side was a plywood panel with bolted door to permit access to the interior. Adult weevils were first reared in a laboratory insectary, then transferred to a screw-cap jar fitted to a hole in the panel: the adults were then free to move onto the enclosed trees through the open mouth of the jar.

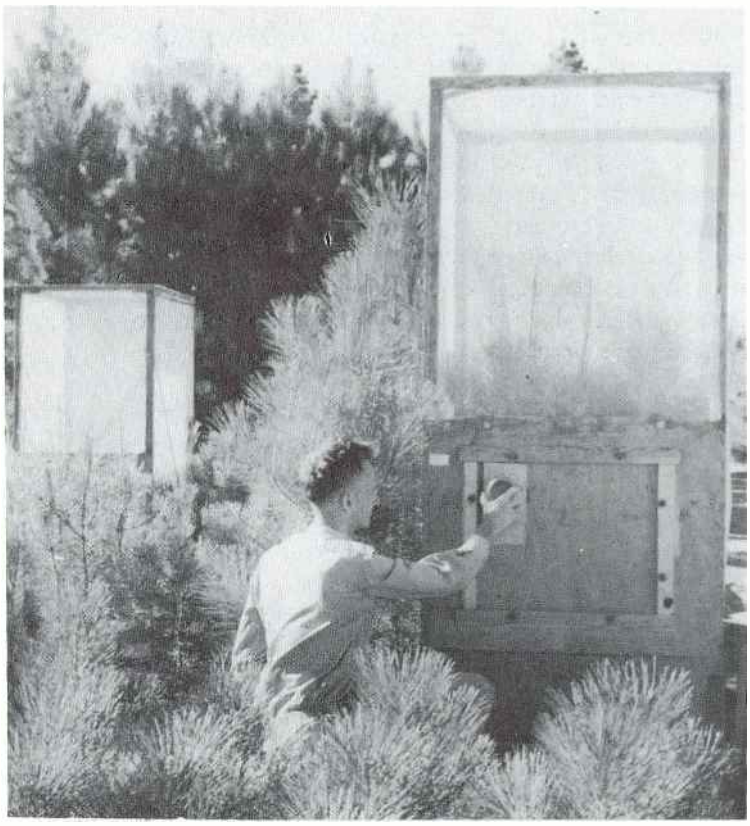


Figure 7.--Cages used for holding weevil populations on selected pines.

Outside the cages, an endemic infestation of the pine reproduction weevil was present in the area around the Institute. It attacked a number of trees in the nursery and arboretum. The activity of this uncaged weevil population furnished valuable data in addition to that obtained from the cage controls, especially on host preference, because adults were free to select only trees which they preferred to attack.

Progress of the attacks which developed in the cages was followed closely each season. At intervals throughout the summer, trees were selected, removed from the cage, and sectioned for microscopic study. Both attacked and unattacked pines were studied to correlate the different stages of weevil development with the nature and extent of weevil-caused injuries in the outer and inner bark.

RESISTANT AND SUSCEPTIBLE PINE STRAINS

The results of 32 separate cage tests and a large number of observations on uncaged attacks in this study point out wide differences among pine species and hybrids, both in host preference shown by the weevil, and in the capacity of trees to resist attack. Briefly summarized these are:

1. Coulter pine is the most resistant of all trees that were tested. Although very heavy weevil populations were forced to attack Coulter pines in the cages, no trees were killed. Outside the cages, the adult weevils were attracted to other pine species but did not attack Coulter pines.

2. Ponderosa and Jeffrey pines were found to be generally susceptible, but between individual trees of each species there was wide variation in resistance to weevil attack.

3. The Jeffrey-Coulter hybrid was not killed by forced attacks in cages. Outside the cages, some of these hybrids were attacked by the weevil but all trees resisted successfully. The capacity of this hybrid to resist weevil attack was comparable to that of Coulter pine.

4. Scopulorum pine (P. ponderosa, var. scopulorum) from the Rocky Mountain region was found to be highly susceptible. Uncaged weevils manifested a high preference for this variety and for hybrids in which scopulorum pine was one of the parent strains.

5. Other species and hybrids of two and three-needle pines which exhibited considerable susceptibility are P. Banksiana, P. washoensis, P. Murrayana x P. Banksiana, P. ponderosa x P. ponderosa var. scopulorum, P. ponderosa x P. apacheca, and P. ponderosa x P. arizonica.

6. Two species of five-needle pines, P. lambertiana and P. torreyana were attacked by the weevil under cage control, but no larvae completed their development.

7. Resistance to weevil attack apparently is not a stable character is some pine species. In Jeffrey pine it was found that one group of trees which resisted strong attacks in 1947 were all susceptible and were killed in 1948; in one nursery bed P. washoensis was susceptible in 1946, but trees were resistant in 1948 when further tests were made. These cases indicate that changes in the physiological condition of a tree may result in susceptibility.

   In Coulter pine and the Jeffrey-Coulter hybrid, which showed strong resistance during all three seasons in which these trees were tested, resistance appears to be an inherited character which is not lost because of such seasonal changes.

SIMILARITIES AND DIFFERENCES OF RESISTANT AND SUSCEPTIBLE PINES

The overall results of the tests show that in certain species of pines some individual trees were killed by the weevil while others, under apparently identical conditions, survived. Between different species and hybrids, some were consistently resistant, others susceptible.

Why were the resistant trees able to resist weevil attack? We can not assume that adult weevils do not like resistant trees and therefore attack them only lightly or not at all. It was demonstrated that under cage controls the adult weevils attacked all enclosed trees impartially, and that progress of the attack was similar throughout the first stages, including oviposition, incubation of the eggs and the first larval instar. From this point on differences between resistant and susceptible trees became readily apparent in the development of the insect and the injury to plant tissues. The explanation for resistance and susceptibility must be somewhere in the processes that go on during the period of early larval development in those layers of living plant cells that are between the outer bark and the sapwood, i.e. the cortex, phloem, and cambium.

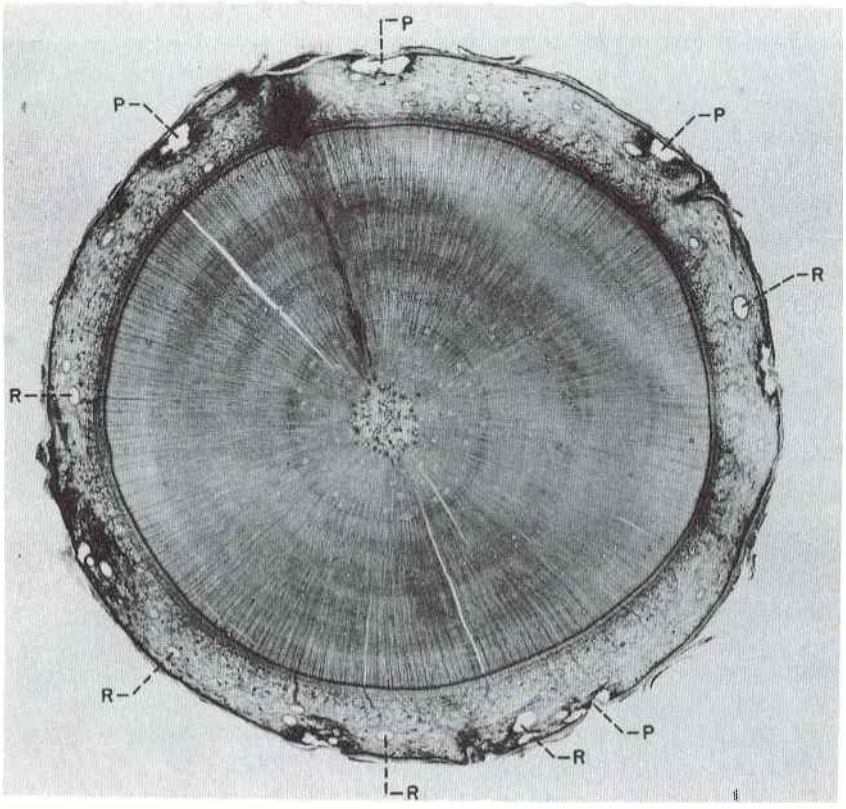


Figure 8.--Cross-section of ponderosa pine stem about one week after attack by weevil.

Punctures

If we examine a cross-section of a pine stem during the first week or two of weevil attack, a number of cavities will be found in the cortex area of the bark. Some of these which are smoothly lined with special cells, are the resin storage vessels (R - in figure 8). Other holes in the outer cortex have roughened margins bordered with shredded cells. These are the cavities cut by the weevil under and around the punctures it makes through the bark surface. At this stage, the extent of the injury appears to be limited to effects of chewing by the adult weevil, which destroys some of the plant cells and causes the death of others immediately adjacent to the cavity that it excavates.

Adult weevils continue their activity on the stems during July and most of August. During this time they continue to make new punctures in the bark. In some trees the bark becomes well perforated with these tiny holes, as many as 100 having been counted on a linear inch of stem.

Most of the punctures are made apparently for the purpose of enabling the adult to feed on the green cortex under the bark surface, but some are also used for oviposition. Only about one out of four punctures produce resin flow; pitch globules occur only where the resin vessels are severed.

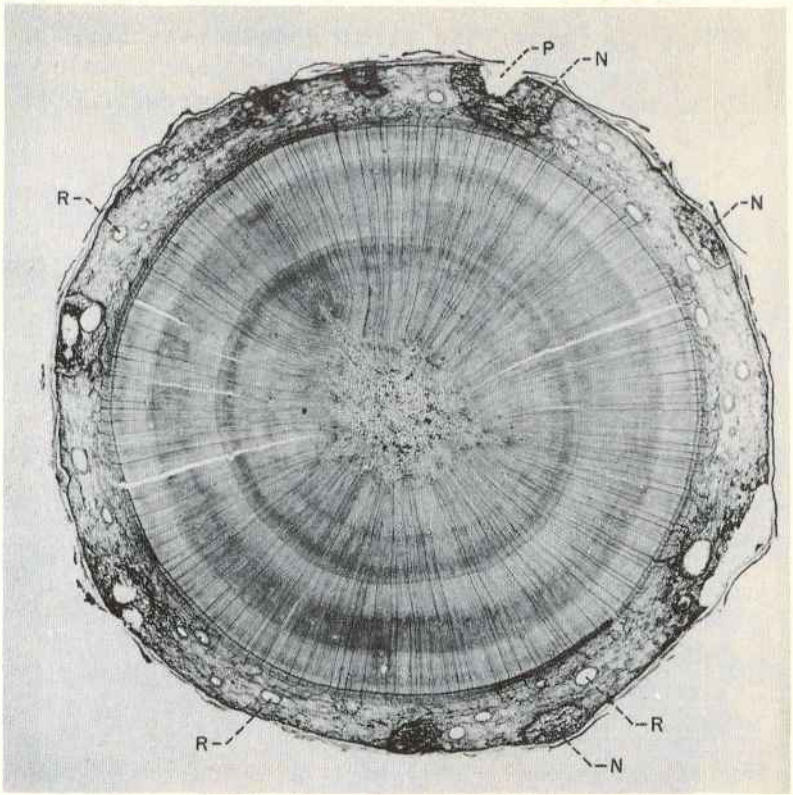


Figure 9.--In about two weeks necrotic areas begin to appear around the first punctures.

Necrotic Areas

If the stem is cross-sectioned after the attack has been in progress for about 15 days, (fig. 9) the resin vessels (R) and the puncture cavities (P) will still be found; but in addition, areas of dead, resin-impregnated cells will be found extending into the cortex around the punctures. These reddish-brown patches have been termed necrotic tissue. It is at about this stage that eggs of the weevil begin to appear in or alongside of necrotic areas.

The cause of this necrotic tissue, except for the effects of the mechanical rupture of plant cells by the weevil, has not been determined. Certainly the rate and extent to which they spread into the living cortex suggests fungus or virus activity. This is a point calling for further study. In any case, necrotic tissue seems to be quite important to the first stage of larval development. Immediately after the egg incubates, the larvae feeds either in, or alongside of a necrotic area. No successful larval development has been found where necrotic areas do not occur.

Around some punctures the necrotic area becomes quite extensive, forming an irregular dark brown patch which can be seen under the outer bark; other areas are very small. Figure 10 shows a ponderosa pine stem with the outer bark peeled off to expose the variable and irregular size of necrotic areas in the cortex. The areas also vary in depth, but most of them are contained in the cortex. Some may penetrate as far as the phloem layer.

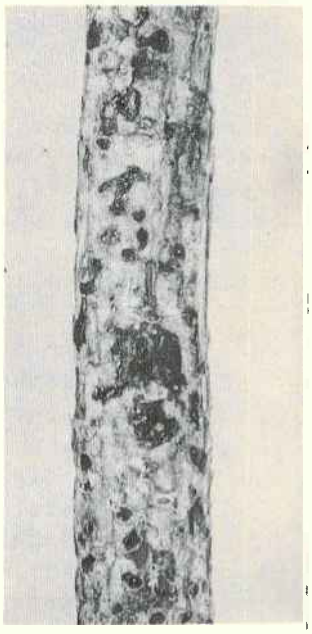


Figure 10.--Pine stem with outer bark removed to expose dark areas of necrotic tissue.

Cork Layers

One of the first growth reactions of the tree to weevil attack is the forming of a layer of cork cells under necrotic tissue. This serves to wall off further spread of necrosis into the living cells of the cortex.

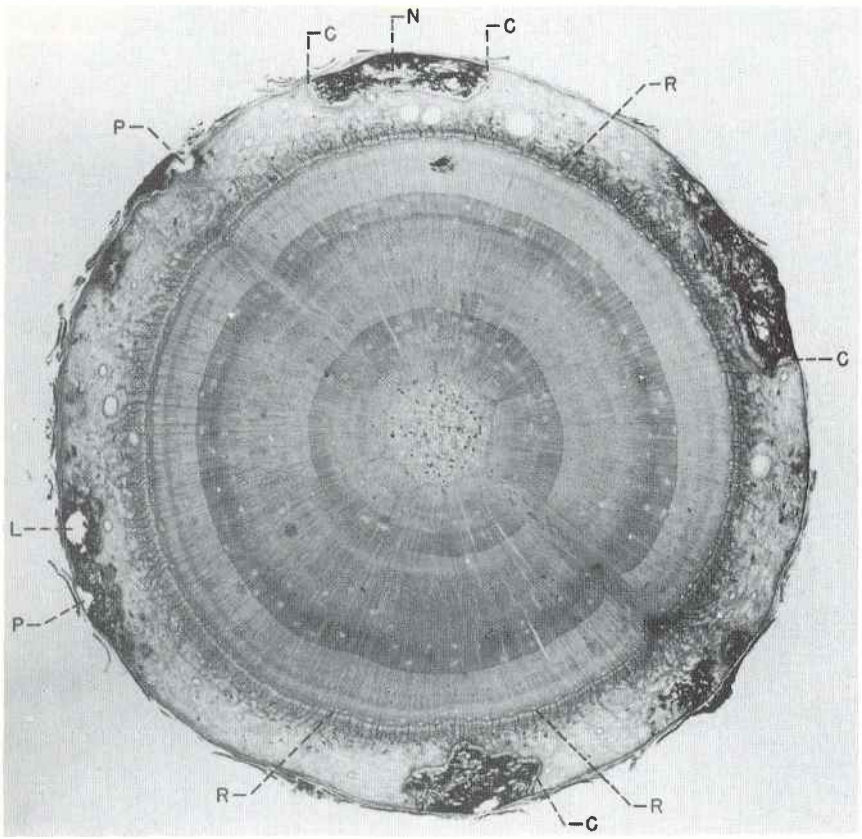


Figure 11.--Thirty days after attack began some necrotic areas are walled off by cork cells, resin ducts are forming, and first larval mines appear - (ponderosa pine).

After the attack has been in progress for 30 days (fig. 11) we find a well formed layer of white cork cells (C) enclosing the necrotic areas. Present also is a concentration of newly formed resin ducts (R) just under the cambium on the outer wood ring. Formation of these resin ducts obviously is stimulated by the effects of weevil attack. Newly formed ducts can be found in both resistant and susceptible trees. Some susceptible trees, however, fail to produce new resin ducts before they are killed by the attack.

In figure 11 one of the first larval mines (L) appears in a necrotic area. Such mines can be identified by the type of frass left by the larva.

Further Developments in Resistant and Susceptible Trees

No significant differences between resistant and susceptible trees could be detected throughout developments extending up to midsummer, but from here on through the late summer and fall, striking differences were easily apparent.

In resistant trees, neither larval development nor necrosis advanced beyond the stage illustrated by figure 11. Throughout the fall and winter the larvae remained within the necrotic areas and made little perceptible growth; or, if they attempted to extend their mines into the living cortex, they soon died. In either case all larvae were dead by the time the tree resumed growth the following spring.

In susceptible trees, the larvae soon left the necrotic areas, extended mines through the living cortex and phloem, rapidly completed their development and the tree died by fall.

Final Phases of Attack in Susceptible Trees

Figure 12 shows a cross-section of a ponderosa pine stem about 50 days after it was attacked by the weevil. This tree is not resisting.

One larval mine (L-2) has broken through the cork layer (C) and has reached the sapwood. General darkening of the phloem and cambium areas indicates that the tree is already dying or dead. Several larval mines (L) are still contained in the necrotic areas.

This tree did not form new resin ducts during the period of attack although a considerable number (R) appear in the wood growth of the preceding seasons.

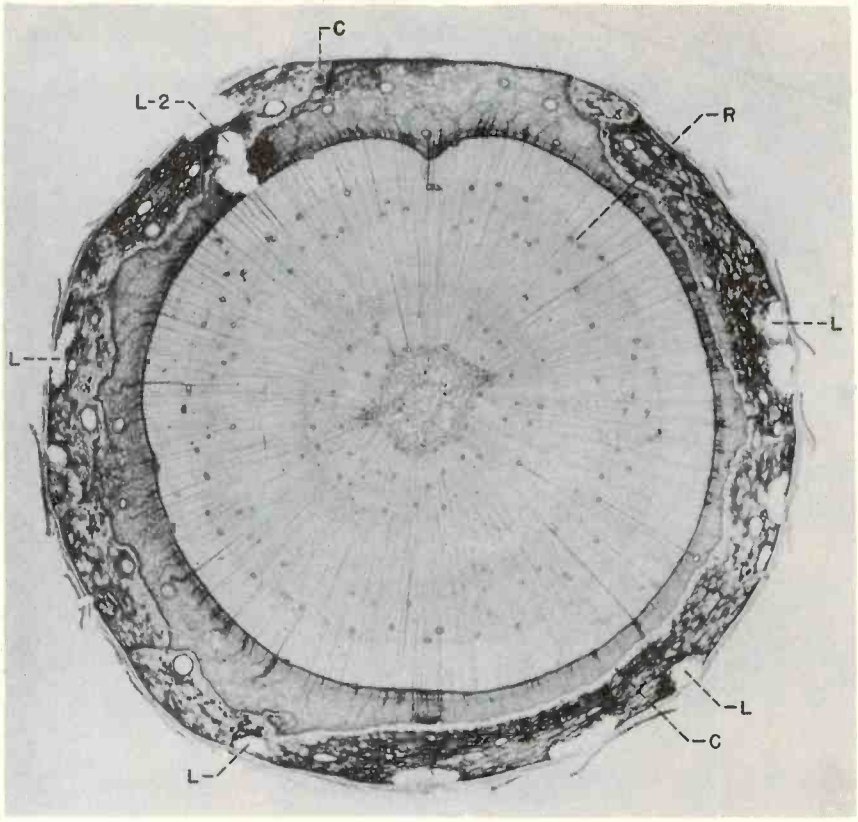


Figure 12.--Weevil larvae have broken out of necrotic areas and extended mines through the cortex and phloem to the wood.

Figure 13 shows the cross-section of a Jeffrey pine stem 90 days after the tree was first attacked by the weevil. This tree is entirely dead as shown by the heavily stained, blackened areas of phloem and cambium.

The larvae are now full grown (September 25). One larval mine (L) in this section extends from the cortex down into the wood where the larva makes its over-wintering cell.

This tree formed new resin ducts (R) during the period of attack, indicating that for a time it was resisting. However these ducts are considerably smaller than those found in strongly resistant trees.

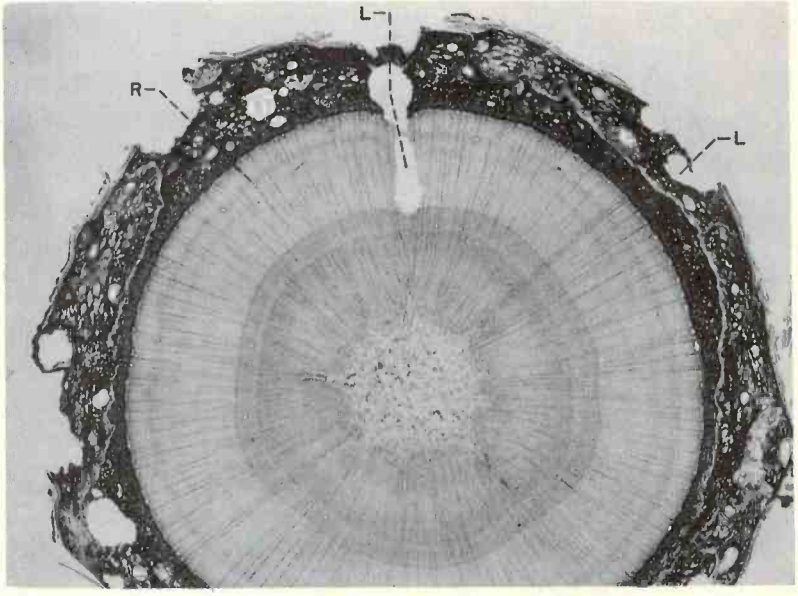


Figure 13.--Larvae have completed their growth and have burrowed into the wood to over-winter.

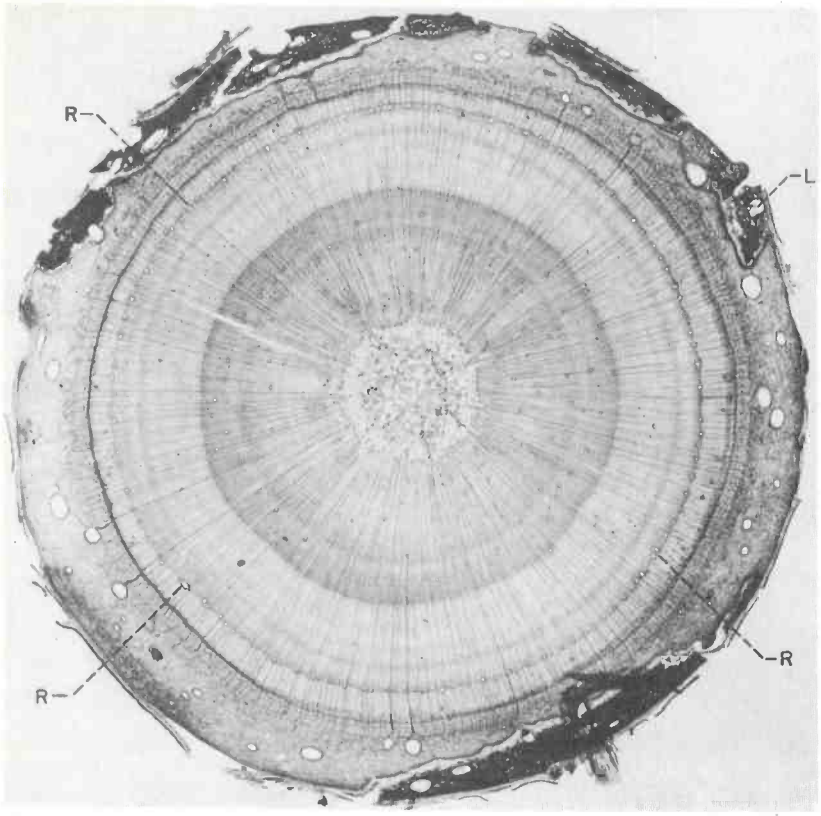


Figure 14.--This ponderosa pine has resisted weevil attack and continued its growth.

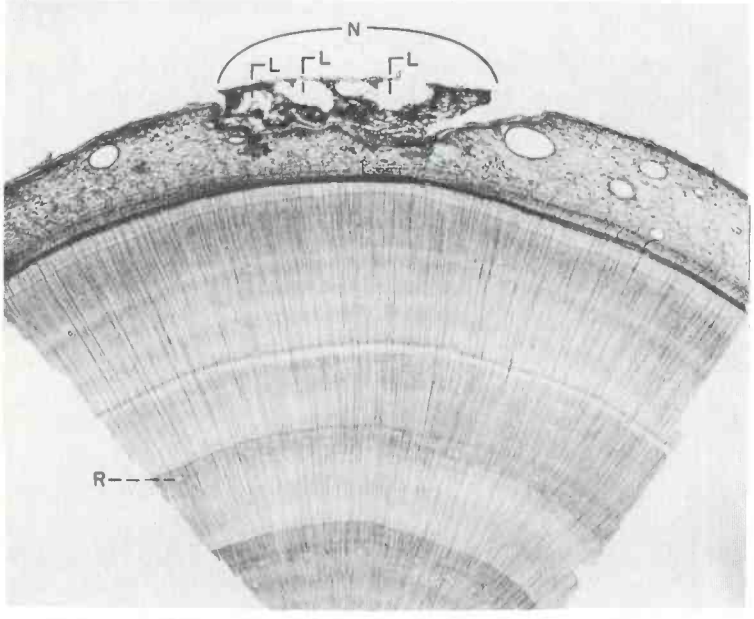


Figure 15.--Remains of a necrotic area on a resistant Jeffrey-Coulter hybrid. This section was taken two years after the attack.

Figure 14 shows a cross-section from a tree that was attacked in July 1947; the section was taken in May 1948, about one month after the tree had started its spring growth. The necrotic areas, which have been completely walled off by cork cells, contain a few small larval mines (L), but no living larvae were found.

This tree formed a heavy concentration of resin ducts (R) on the wood surface during the period of attack, but this ring of resin ducts is now covered by new wood growth of the 1948 season.

Figure 15 is taken from the stem of a resistant Jeffrey-Coulter hybrid which was attacked by the weevil in June 1946. The section was taken in June 1948, approximately 2 years later. New cortex tissue has formed under the old necrotic area (N), and the dead necrotic tissue is now being pushed out to the bark surface where it will eventually be sloughed off.

Larval mines (L) can still be seen in the old necrotic area, but it is evident in this case that the larvae were unable to extend their mines into the living cortex before they died.

A faint concentration of resin ducts (R), which may have been stimulated by the attack, appears in the two-year-old wood growth.

FACTORS CONTRIBUTING TO SUSCEPTIBILITY OF PINES

The great variability in resistance to the weevil found among species and individuals of pines included in this study indicates that the host-insect relationship in this case is not a simple one. It can reasonably be assumed that all pine species growing within the range of weevil populations possess some degree of resistance; otherwise these species would eventually be exterminated by the insect. Among these are species, such as Coulter pine, which seem to possess almost complete immunity because of undetermined inherited characteristics in their cellular and biochemical make-up; other species show a variable degree of resistance, suggesting that unfavorable environmental factors may bring about changes in the physiological condition of living trees, changes which weaken the capacity to throw off the attack.

This field was not explored in the present studies, but some observations may have a bearing on causes of susceptibility in pines that would otherwise resist weevil attack.

Resin Production

Not only did attack by the weevil cause a flow of resins from ruptured storage vessels in the cortex to the outer bark surface, but it also stimulated in many trees the formation of new resin ducts in the outer wood ring. These new ducts, however, did not appear until the attack had been in progress for 15 to 30 days.

Some susceptible trees failed to form any noticeable concentrations of these new ducts (fig. 12); other susceptible trees formed small but definite ducts (fig. 13).

The formation of new resin ducts was most pronounced in resistant trees. Figure 16 is a cross-section of a Coulter pine stem which resisted attack in June, 1947; the section was taken in October of the same season. In this section necrotic tissue extends in a connected band around the entire outer circumference, is completely walled off by cork cells, but does not penetrate deeply into the cortex. The few larval mines that are present have been contained within the necrotic areas.

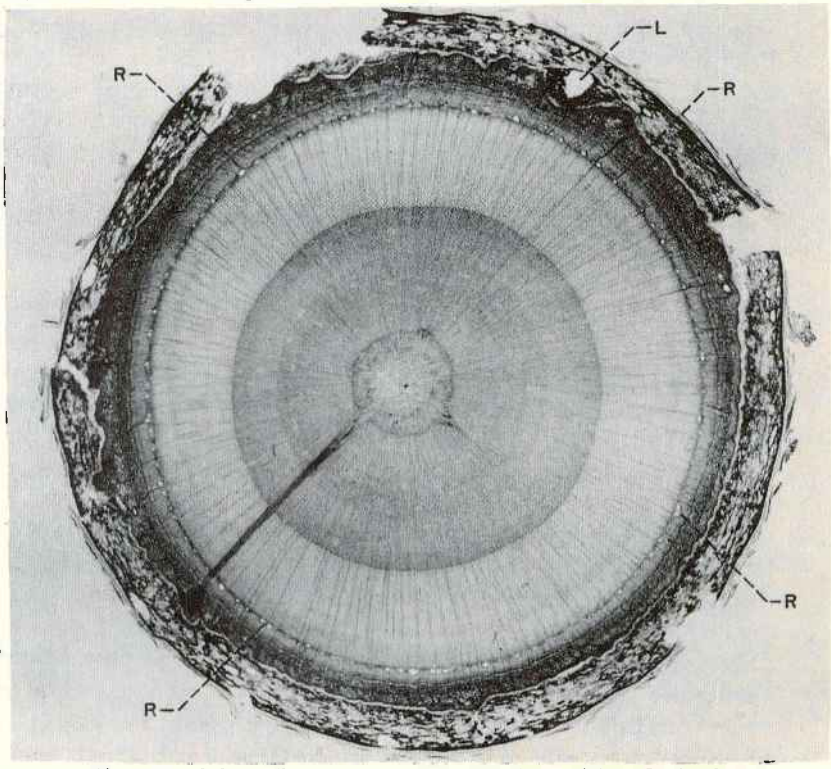


Figure 16.--Large resin ducts stimulated by weevil attack on Coulter pine.

A prominent feature of this section is the ring of large resin ducts (R) that formed during progress of the attack. This tree continued to lay down wood cells after the resin ducts were formed so that they are now imbedded in the seasonal growth ring.

Part of the resins produced in the wood are transferred through medullary rays to the cortex, and it is here that they contact the young larvae in weevil-infested trees. Both the quantity and the chemical components of the resins that are produced following attack may prevent extension of larval mines into the living cortex. It was noted that larvae that had died while attempting to mine the cortex area were usually found to be encased in gummy resin masses which filled their mines.

The capacity of a tree to produce the resins necessary to arrest weevil attack may therefore be an index to its resistance to weevil attack. A study of the nature of the resins stimulated by attack and their effect upon the larval stages of the weevil is needed to clarify the role of resin production and to determine whether or not failure to produce such resins results in susceptibility.

Growth Vigor

Both Coulter pine and the Jeffrey-Coulter hybrid have shown unusual growth vigor as compared with ponderosa and Jeffrey pines. With this in mind, it is easy to assume that growth vigor is a dominant factor in weevil resistance, but other cases on record do not lend support to this theory. It was found that some small suppressed ponderosa pines successfully resisted attack while fairly vigorous trees were killed. In one test a Jeffrey pine of unusually high vigor was killed by forcing a heavy weevil population to attack it. On the whole, however, the faster growing trees in these tests have shown more resistance than the slower growing trees, indicating that growth vigor operates either directly or indirectly to the disadvantage of the weevil.

Soil Moisture

Sudden slowing down of growth rate may be highly important in the susceptibility of young pines to weevil attack. Deficiencies of soil moisture obviously affect adversely the growth conditions of a tree, and it was demonstrated in one case that this factor may operate to change individual trees from a resistant to a susceptible condition. In 1947 a cage test was run on 14 Jeffrey pines which were irrigated during the summer under the nursery sprinkler system. All trees survived strong weevil attacks. The next season, 1948, the same trees were subjected to a similar test and all were killed. The only difference in conditions between the two years was that irrigation was discontinued in 1948. It is believed that lack of water, combined perhaps with injuries received during the first year of attack, explains the change from resistance to susceptibility in this group of trees. The moisture theory is further supported by the fact that outside the cages weevil infestations increased in 1948 in those nursery beds where irrigation was discontinued.

FURTHER WORK NEEDED

Planting Tests

In the cages and under nursery conditions, the Jeffrey-Coulter hybrid has shown a capacity to resist weevil attack comparable to that of Coulter pine. This hybrid, in addition to weevil resistance during its early growth is expected to produce acceptable wood quality because of its Jeffrey parent. It should therefore be desirable for planting in brushfield areas where ponderosa and Jeffrey pines have failed to survive weevil infestations. However, field plantings may involve some factors not encountered in the preliminary tests described in this paper, and for this reason test plots are highly desirable in the areas where large-scale planting is contemplated. A start toward this objective was made in the spring of 1948 when three one-acre plots of the Jeffrey-Coulter hybrids and its parents were set out in the northern California brush-fields. Several more years of growth will be required before these planted trees can be tested by weevil populations and results of the test plantings can be made available.

Important Basic Studies

Studies of those factors that contribute to resistance or susceptibility of pines to weevil attack have a wide application in other problems of forest entomology. Attempts to explain the behavior of barkbeetle infestations have encountered obscure, underlying factors that affect the growth functions of living trees in such a manner as to induce susceptibility to insects that feed in the inner bark. The pine reproduction weevil provides an excellent medium for such studies because growth conditions in the young trees that it attacks can be recognized and controlled more easily than in mature trees.

Later on, as some of the new strains of pines now growing in the outplantings of the Institute of Forest Genetics arrive at suitable age for barkbeetle attack, tests can be made of their resistance to Ips and Dendroctonus beetles that are well established enemies of older pines. In this field also the Jeffrey-Coulter hybrid presents an interesting case for study, because its Coulter parent is susceptible to the western pine beetle (Dendroctonus brevicomis) while its Jeffrey parent is not; on the other hand Dendroctonus jeffreyi attacks only Jeffrey pine and there is no record of its attack on Coulter pine. The reactions of the beetles, when they encounter the mixture of favorable and unfavorable host strains in this hybrid should be well worth following.